more or less during tissue differentiation and, therefore, tend to be considerably longer than the vessel members and than the cambial initials from which they are both derived. The tangential diameters of the imperforate tracheary cells are determined largely by the cambial initials. Therefore, conspicuous fluctuations in the cross-sectional area of imperforate tracheary elements are commonly correlated with variations in the size of the fusiform initials of the cambium.

As we have shown in the preceding paper of this series and as is indicated in Table I, there is a progressive shortening of the vessel members and pari passu of the fusiform initials of the cambium with increasing structural specialization of the vessels in the Icacinoideae. If the amount of elongation of the imperforate tracheary elements were the same in all cases, the phylogenetic shortening of the vessel members would of necessity be closely paralleled by a concomitant decrease in length of the imperforate elements. It is evident, however, from the measurements listed in Table I that the elongation of these cells varies in different categories of the Icacinoideae.

TABLE I

MEASUREMENTS IN MICRONS

Categories of Icacinoideae	Average length cambial initials vessel members	Average length imperforate tracheary cells	Average Elongation imperforate tracheary cells
I. Trilacunar Icacineae: scalariform	1470	2490	1020
II. Trilacunar Icacineae: scalariform-porous	1050	2580	1530
III. A. Unilacunar Icacineae: porous	590	1600	1010
III. B-D. Iodeae, Sarcostigmateae, Phytocreneae: porous	470	870	400

In the group II Icacinoideae, the imperforate tracheary elements are on an average slightly longer than those of Group I. This is due to the fact that, although the cambial initials of Group II are conspicuously shorter than those of Group I, the imperforate tracheary elements elongate more extensively during tissue differentiation. In Group IIIA, the elongation of these elements is comparable to that in Group I, but the cells are much shorter owing to excessive decrease in the length of the cambial initials. In Group IIIB-D, the imperforate tracheary elements are very short due not only to a further decrease in the length of the cambial initials but also to a reduced elongation during tissue differentiation. It is evident, accordingly, that in the Icacinaceae, as in certain other families of dicotyledons, the specialization of the vessels must be of considerable magnitude before a statistically significant shortening of the imperforate tracheary elements becomes evident.

Although the imperforate tracheary elements of the Group II Icacinoideae are as long and have as large a cross-sectional area as the tracheids of Group I, they commonly exhibit a conspicuous reduction in the size of their bordered pits and in the volume of their lumina. In such genera of the Group I Icacinoideae as *Anisomallon, Apodytes, Calatola, Cassinopsis, Dendrobangia, Emmotum, Oecopetalum, Pittosporopsis, Platea, Poraqueiba,* and *Citronella,* the inter-tracheid bordered pits commonly attain maximal diameters of from 4–5μ in the first-formed secondary xylem and from 6–8μ in the later-formed wood. These pits have clearly defined borders in surface view and large conspicuous chambers in sectional view, *Figs. 1 & 2.* In the Group II Icacinoideae, bordered pits of comparable dimensions occur in certain species of *Stemonurus* and *Cantleya,* but less commonly, if ever, in *Discophora, Gastrolepis, Grisollea, Gonocaryum, Lasianthera, Leptaulus, Medusanthera,* and *Urandra.* In the latter genera, not only are the borders of the pits more or less reduced in diameter, *Fig. 3,* but also the pit chambers frequently are flattened and thus are difficult to detect in sectional views of the bordered pits.

In the Group I Icacinoideae, the walls of the tracheids fluctuate from relatively thin in *Platea, Fig. 1,* to very thick in *Apodytes, Emmotum, Fig. 2, Ottoschulzia* and certain species of *Citronella.* In the Group II Icacinoideae, with the exception of *Gonocaryum* and of certain species of *Leptaulus* and *Stemonurus,* the lumina of the imperforate tracheary elements are much reduced in volume or are occluded by excessive thickening of the secondary walls, *Fig. 3.*

In the Group IIIA, in contrast to the Group I, Icacinoideae, the imperforate tracheary elements of the arborescent and non-scandent frutescent species exhibit not only a marked decrease in length and in cross-sectional area, *Fig. 4,* but also a conspicuous reduction in size of the bordered pits. The latter trend of specialization is, however, less advanced in *Merrilliodendron* than in *Desmostachys* and *Alsodeiopsis* and particularly than in *Mappia* and *Nothapodytes.* In the last two genera, the bordered pits have been reduced to simple ones and the transition to libriform fibers is complete, *Fig. 4*. On the contrary, in those representatives of the unilacunar Icacineae having a scrambling or climbing habit of growth, as in the scandent Iodeae, Sarcostigmateae and Phytocreneae, there are reversals in the specialization of the imperforate tracheary elements which culminate in the formation of curious short tracheids. These tracheary cells are characterized by having relatively conspicuous lumina and numerous large bordered pits. They are most typically developed in the large-vesselled anomalous wood of *Pleurisanthes, Lavigeria* and of various representatives of the Iodeae and Phytocreneae. Intermediate or transitional stages of their phylogenetic differentiation occur in *Humirianthera, Icacina, Leretia, Rhaphiostylis, Mappianthus* and *Sarcostigma,* as well as in the denser, smaller-vesselled parts of the stems of certain Iodeae and Phytocreneae.

WOOD PARENCHYMA

The terminology of wood parenchyma distribution has been and still is somewhat confused and unsatisfactory, and ultimately will have to be revised and clarified. Although a comprehensive revision should not be attempted until more adequate data are available, certain recently proposed modifications of the terminology should be discussed at this time.

There are obviously two fundamentally different categories of wood parenchyma distribution. In the first of these, the distribution bears no specific relationship to the vessels, i.e. contacts between parenchyma and vessels are random and indefinite. On the contrary, in the second type, the parenchyma is definitely aggregated about the vessels. Chalk's (4) suggestion that these two major categories be designated respectively as *apotracheal* and *paratracheal* is, therefore, deserving of careful consideration. Chowdhury (5) has advocated the term, initial, for use in contrast to terminal, and Kribs (6) has proposed two additional terms, diffuse-aggregate and banded paratracheal. If these suggestions were generally adopted, the following classification of types of parenchyma distribution would result:

Apotracheal	**Paratracheal**
diffuse	scanty paratracheal
diffuse-aggregate	banded paratracheal
metatracheal	confluent
terminal	aliform
initial	vasicentric

Such a classification, however, is open to criticism from various angles. The term, metatracheal, was originally used by Sanio (7) for types of distribution in which the vessels are linked together by parenchyma. To use this term for designating an apotracheal type of distribution reverses the original meaning and it appears desirable to replace it by *banded apotracheal.* To make diffuse-aggregate of coordinate rank with diffuse and to confine the use of the latter term to woods in which the wood parenchyma strands are completely isolated from one another is both unnecessary and unwise; woods are classified as diffuse porous regardless of whether the individual vessels are isolated or occur in small clusters. Diffuse-aggregate or preferably *diffuse-in-aggregates* should be used in designating one of several possible sub-divisions of diffuse. In the case of tropical woods, there frequently is considerable difficulty in differentiating banded apotracheal from terminal. The introduction of the term, initial, further complicates the difficulty. Terminal has been utilized from a descriptive or topographical point of view for parenchyma situated at or upon the margins of growth layers, regardless of whether it differentiates at the end or the beginning of a growing season. To interject a purely ontogenetic point of view at this time is inadvisable.

Kribs' (6) statistical investigations have demonstrated that the primitive type of parenchyma distribution in dicotyledons is diffuse and that the aggregation of parenchyma in apotracheal bands and in paratracheal patterns involve varying degrees of phylogenetic specialization. It should be emphasized in this connection, however, that the statistical data do not enable one to determine with certainty how the various paratracheal types have arisen from the apotracheal ones. This can be accomplished only by intensive investigations of a wide range of families. Recent unpublished investigations of this character indicate that (1) broad-banded apotracheal types arise from diffuse ones through various transitional narrow-banded apotracheal types, (2) in many families, vasicentric, aliform and confluent types originate from banded types, and (3) through excessive reduction, scanty paratracheal types may arise at various levels of the differentiation of both apotracheal and paratracheal types. Furthermore, these investigations indicate that there are many complex types of parenchyma distribution which are transitional between typical apotracheal and purely paratracheal types. These distributional patterns are so diverse and variable, not only in related genera and species but also within the limits of a single individual, that it seems unwise to develop a fixed and stereotyped terminology for their description.

In view of such facts as these, we propose to use the following simplified basic terminology:

Apotracheal (Chalk)	**Paratracheal** (Sanio)
diffuse	scanty
banded	abundant
terminal	abaxial
	vasicentric

The more complex transitional types of distribution will be referred to as such. For example, banded paratracheal will be regarded as a mixture of banded apotracheal and paratracheal just as diffuse may be associated with paratracheal, terminal with vasicentric, etc. Confluent and aliform will likewise be regarded as transitional or mixed types. Furthermore, the definition of confluent either should be revised or the term should be used in a purely descriptive sense without implication of origin from coalesced aliform.

The distribution of the wood parenchyma in the Group I Icacinoideae is dominantly of the primitive diffuse apotracheal type, *Fig. 5*. The parenchyma is abundant and tends to occur in small linear aggregates of varying sizes, forms and orientations.[1] Where the parenchyma is reduced in amount, as in the small stems of certain herbarium specimens, there is at times a higher ratio of contacts between parenchyma and vessels than can be accounted for upon the basis of a purely random distribution of the parenchymatous elements. This tendency is much exaggerated in the wood of *Emmotum holosericeum* Ducke and certain exceptional species of *Citronella,* where the distribution is obviously transitional to scanty paratracheal and much of the parenchyma tends to be in contact with the abaxial surfaces of the vessels. In *Poraqueiba, Fig. 6,* and particularly in *Ottoschulzia,* there frequently are indications of transitions from diffuse (in tangentially linear aggregates) to narrow-banded apotracheal.

The distribution of wood parenchyma in the Group II Icacinoideae is transitional and highly variable. In *Stemonurus, Discophora* and *Gonocaryum,* the parenchyma is abundant and tends to be transitional between diffuse (in tangentially linear aggregates) and narrow banded apotracheal.[2] In *Medusanthera,* the parenchyma is transitional between these types of distribution and more or less irregularly banded types in which the vessels are partly or completely jacketed by parenchyma, *Fig. 9.* In *Cantleya*[3], *Gastrolepis* and *Urandra*[4], the parenchyma is scanty paratracheal, but exhibits vestiges of its derivation from apotracheal, *Fig. 10.* In the wood of *Leptaulus daphnoides* Benth., the distribution is transitional from diffuse to very scanty paratracheal, and the parenchyma tends to occur in contact with the abaxial surfaces of the vessels, *Fig. 11.* In small stems from herbarium specimens of *L. grandifolius* Engl., *L. Zenkeri* Engl., and *Grisollea Thomassetii* Hemsl., there are conspicuous arcs of aggregated vessels and parenchyma in the first-formed secondary xylem. However, this is not indicative necessarily of a similar distribution in the later-formed wood. Aberrant distributions of vessels and parenchyma are of not infrequent occurrence in young stems, particularly where growth is excentric or where tropistically induced arcs of gelatinous fibers are formed.

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[1] For additional illustrations of these types of parenchyma distribution, the reader is referred to *Figs. 1–3* of the preceding paper of this series, Bailey & Howard (3).

[2] See *Fig. 6* of the preceding paper of this series.

The wood parenchyma of the Group III Icacinoideae occurs in varying mixtures of apotracheal and paratracheal types of distribution and the ratios of the two types fluctuate greatly not only in different genera and species but also in different parts of the same plant. *Merrilliodendron* is characterized by having very abundant apotracheal parenchyma, *Fig. 7.* It is transitional between diffuse (in tangentially linear aggregates) and narrow-banded apotracheal and occurs in association with paratracheal parenchyma which encloses the vessels, viz., vasicentric. Similar distributions of apotracheal parenchyma occur in certain representatives of *Nothapodytes,* whereas in others, as in *Mappia, Fig. 14,* and *Alsodeiopsis, Fig. 8,* the distribution is of a more or less irregular banded apotracheal type. In these plants, the associated paratracheal parenchyma fluctuates between scanty and vasicentric. It should be noted in this connection, however, that there are certain species of *Nothapodytes,* e.g. *N. dimorpha* (Craib) Sleumer and *N. pittosporoides* (Oliv.) Sleumer, which are structurally divergent. Twigs from herbarium specimens of these plants are characterized by having fairly conspicuous growth layers and small vessels in relatively large irregular clusters. The vessels have conspicuous spiral thickenings and the parenchyma is much reduced in amount, occurring as fragments of bands and as scattered isolated cells.

In our material of *Desmostachys, Fig. 12,* and of those unilacunar Icacineae which have a scrambling or climbing habit of growth, viz., *Icacina, Humirianthera, Lavigeria, Leretia, Pleurisanthes, Fig. 15, Rhyticaryum* and *Rhaphiostylis, Fig. 13,* there is a more or less conspicuous reduction in the amount of banded apotracheal parenchyma. The associated paratracheal parenchyma tends to persist as the apotracheal is reduced, and thus there are varied transitions between mixed banded apotracheal and paratracheal types of distribution and others having a prevailingly paratracheal or vasicentric distribution. Such fluctuations are of common occurrence in different parts of the same plant, and it is difficult to characterize species or genera by specific types of parenchyma distribution. As the banded apotracheal parenchyma is reduced in amount, it tends to be replaced by shorter and shorter arcs of parenchyma, varying ratios of which are closely associated with the vessels. Under the latter circumstances, the paratracheal parenchyma appears to have winglike or aliform extensions, *Figs. 12 & 13*. This is true regardless of whether the vessels are completely jacketed by paratracheal parenchyma or not.

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[3] See *Fig. 4* of the preceding paper of this series.

[4] See *Fig. 7* of the preceding paper of this series.

Similar unstable types of parenchyma distribution occur in the less specialized, small-vesselled parts of the stems of certain representatives of the Phytocreneae and the Iodeae, e.g. *Mappianthus, Hosiea sinense* (Oliv.) Hemsl. & Wils., *Iodes liberica* Stapf, etc. In the large-vesselled anomalous wood of these plants, as also of *Pleurisanthes* and *Lavigeria,* the parenchyma tends to be more dominantly paratracheal, *Fig. 16,* and occurs in association with much modified vestiges of banded apotracheal. In *Sarcostigma* and at times in certain of the Phytocreneae, the strands of wood parenchyma tend to be replaced by curious septate fusiform parenchymatous elements; true septate fibers do not occur in the secondary xylem of the Icacinoideae.

It should be noted, in connection with our discussion of wood parenchyma, that the length of parenchyma strands and of fusiform parenchymatous elements is determined by the length of the fusiform initials of the cambium. Therefore the reductions in the length of the vessel members and of the cambial initials in the Group II and Group III Icacinoideae are closely paralleled by concomitant reductions in the length of the parenchymatous elements.

SUMMARY AND CONCLUSIONS

The data presented in the preceding pages indicate that there are salient trends of morphological specialization in the imperforate tracheary elements and the wood parenchyma of the Icacinoideae which tend in general to parallel those that occur in the vessels. Although the phylogenetic modifications of these three categories of cells are not perfectly synchronized in all cases, the differentiation of the Icacinoideae into three Groups, upon the basis of differences in vessel structure, serves to segregate the imperforate tracheary elements and the wood parenchyma into three general levels of increasing morphological specialization.

In our Group I Icacinoideae, as in many other genera of structurally less modified dicotyledons, the primitive types of vessels occur in association with typical large, more or less thick-walled tracheids. In the Group II Icacinoideae, the imperforate tracheary elements do not exhibit a reduction in length owing to their excessive elongation during tissue differentiation, but do show a conspicuous tendency towards reduction in size of their bordered pits and towards a much exaggerated thickening of their secondary walls. In other words, the imperforate tracheary elements of this group exhibit evidences of a transition from tracheids to fiber-tracheids. In the non-scandent representatives of the Group IIIA Icacinoideae, the imperforate tracheary elements show not only a conspicuous reduction in both length and cross-sectional area, but also in the size of their bordered pits which culminates in *Mappia* and *Nothapodytes* in the formation of libriform fibers. In the scrambling and climbing representatives of the Group IIIA Icacinoideae, as in the scandent Iodeae, Sarcostigmateae and Phytocreneae, there is a further reduction in the length of the imperforate tracheary elements and a tendency for enlargement of the bordered pits. These trends of specialization culminate — as in scandent representatives of a number of other families of the dicotyledons — in the formation of curious short tracheids which resemble the vessels in having numerous, large bordered pits.

The distribution of the wood parenchyma in the Group I Icacinoideae is dominantly of the primitive diffuse apotracheal type. However, the most highly specialized representatives of this group — i.e. from the point of view of the vessels — have parenchyma that is either transitional between diffuse and narrow-banded apotracheal, *Poraqueiba* and *Ottoschulzia*, or between diffuse and scanty abaxial paratracheal, *Emmotum*. The parenchyma of the Group II Icacinoideae fluctuates markedly in both abundance and distribution and exhibits several trends of specialization. In *Stemonurus, Discophora* and *Gonocaryum,* it is abundant and is transitional between diffuse (in tangentially linear aggregates) and narrow-banded apotracheal. In *Medusanthera,* it is transitional between these types of distribution and more or less irregularly banded types in which the vessels are partly or completely jacketed by parenchyma. In *Cantleya, Gastrolepis* and *Urandra,* the parenchyma is scanty paratracheal, but exhibits vestiges of its derivation from apotracheal. In the wood of *Leptaulus daphnoides* Benth., it is transitional between diffuse and very scanty, abaxial paratracheal. Most, if not all, of the Group III Icacinoideae are characterized by having more or less paratracheal parenchyma that occurs in association with varying percentages of apotracheal. In *Merrilliodendron, Mappia* and most species of *Nothapodytes,* the apotracheal parenchyma is abundant and is either transitional between diffuse (in tangentially linear aggregates) and narrow-banded apotracheal or is dominantly banded apotracheal. On the contrary, in the scandent or semi-scandent representatives of the unilacunar Icacinoideae, as in the Iodeae and Phytocreneae, the banded apotracheal parenchyma is exceedingly unstable both as regards its abundance and its distributional patterns. In *Sarcostigma* and in certain of the Phytocreneae, there is a tendency to replace the wood parenchyma strands by curious septate, fusiform parenchymatous elements.

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DESCRIPTION OF PLATES

PLATE I.

FIG. 1. *Platea species. Y. U. 20201.* Transverse section of thin-walled tracheids, showing three bordered pits in sectional view. × 1200.

FIG. 2. *Emmotum holosericeum* Ducke. *Y. U. 33816.* Transverse section of thick-walled tracheids, showing bordered pits in sectional view. × 1200.

FIG. 3. *Discophora panamensis* Standl. *Y. U. 12246.* Transverse section of fiber-tracheids and parenchyma, showing pits with reduced borders. × 1200.

FIG. 4. *Nothapodytes obtusifolia* (Merr.) Sleumer. *Y. U. 29539.* Transverse section of libriform fibers, showing simple pits. × 1200.

PLATE II.

FIG. 5. *Apodytes dimidiata* E. Mey. *Y. U. 14833.* Transverse section of the wood. Parenchyma distribution is diffuse-in-aggregates. × 50.

FIG. 6. *Poraqueiba sericea* Tul. *Y. U. 19244.* Transverse section of the wood. Parenchyma transitional between diffuse (in tangentially linear aggregates) and narrow-banded apotracheal. × 50.

FIG. 7. *Merrilliodendron rotense* Kanehira. *Y. U. 19468.* Transverse section of the wood. Parenchyma distribution is a mixture of vasicentric and diffuse-in-aggregates. × 50.

FIG. 8. *Alsodeiopsis Schumanii* Engl. *O. U. 5060.* Transverse section of the wood. Parenchyma distribution is a mixture of banded apotracheal and paratracheal. × 50.

FIG. 9. *Medusanthera samoensis* (Reinecke) Howard. *Y. U. 26117.* Transverse section of the wood. Parenchyma distribution is a mixture of irregularly banded apotracheal and paratracheal. × 50.

FIG. 10. *Urandra scorpioides* (Becc.) O. Ktze. *Y. U. 16043.* Transverse section of the wood. Parenchyma is paratracheal and vestigial apotracheal. × 50.

PLATE III.

FIG. 11. *Leptaulus daphnoides* Benth. *Y. U. 19758.* Transverse section of the wood. Parenchyma is scanty diffuse and abaxial paratracheal. × 100.

FIG. 12. *Desmostachys Vogelii* Stapf. *Y. U. 15097.* Transverse section of the wood. Parenchyma is scanty paratracheal with winglike or aliform extensions of apotracheal. × 100.

FIG. 13. *Rhaphiostylis cordifolia* Hutch. *Linder 1218.* Transverse section of a young stem. Parenchyma is scanty paratracheal and vestigial apotracheal. × 100.

FIG. 14. *Mappia racemosa* Jacq. *Y. U. 12196.* Transverse section of the wood. Parenchyma is scanty paratracheal and broad-banded apotracheal. × 100.

FIG. 15. *Pleurisanthes flava* Sand. *N. Y. 590.* Transverse section of a young stem. Parenchyma is paratracheal. × 100.

FIG. 16. *Iodes ovalis* Bl. *H. U. 2775.* Transverse section of large-vesselled anomalous secondary xylem. Parenchyma is vasicentric. × 100.

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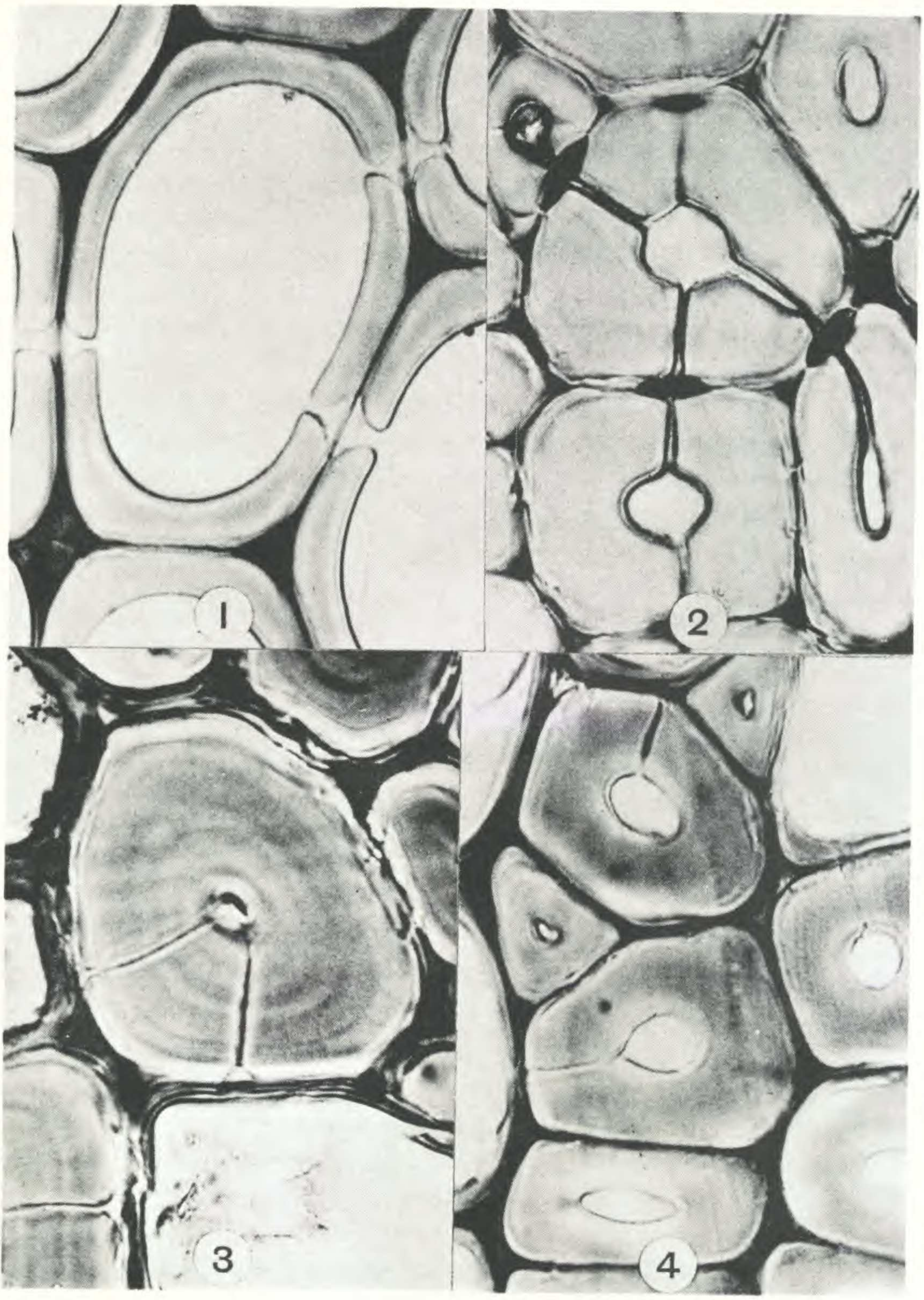

COMPARATIVE MORPHOLOGY OF THE ICACINACEAE

FULL-TONE—MERIDEN